

Butterflies and Biospecies

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Abstract. A reexamination of the biological species concept confirms Ehrlich's 1961 conclusion that it had, by then, outlived its usefulness. This in no way lessens the importance of thinking in evolutionary terms when studying the biology of butterflies.

It seems appropriate, as Shapiro (1983) suggests, to reexamine the conclusions Ehrlich (1961) drew more than two decades ago about the ease of recognizing "biological species" in butterflies. One should do so in the context of what has happened in systematics during that period.

What might be called the "numerical taxonomy revolution," begun by Michener and Sokal's (1957) work with bees and Sneath's (1957a, b) studies of bacteria, as Shapiro indicates, has run its course. It caused a fundamental reevaluation of the intellectual underpinnings of taxonomy, changed forever how detailed (but not routine) taxonomic investigations are done, and led to a reexamination of the biological species concept (BSC). Ehrlich's original conclusions—that the concept was misleading and not very useful—were basically confirmed by Sokal and Crovello's (1970) more detailed examination. Since then, nothing has appeared in the general literature to give any reason for changing those conclusions.

The difficulty with the biological species as a taxonomic category is that, where it might be useful, it is impossible to apply. Biological species were defined by Ernst Mayr (1940) as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". Under that definition the test of whether two phenetically similar forms are part of the same species or of different species is what happens when they occur together *in nature*. Where the forms are sympatric and synchronic, a clear decision *may* be made impossible by partial interbreeding (or, more often, by practical difficulties in determining whether there is interbreeding at all). But insurmountable problems arise when considering allopatric populations, since there is no way to predict what would happen if the two similar forms later became

sympatric (Ehrlich, 1961). And yet *application* of the BSC requires prediction of the potential for interbreeding.

To give a simple example, *Euphydryas editha* populations in the San Francisco Bay area (subspecies *bayensis*) have been isolated from *E. editha* in Colorado (*gunnisonensis*) for at least 7000 generations (Ehrlich and White, 1980). It has been that long since suitable habitat was more or less continuous across the now-arid intermountain region. The two sets of populations feed on different foodplants, adult flights are completely allochronic, and they are genetically and phenetically at least somewhat differentiated (Brown, 1970; Ehrlich et al., 1975; Ehrlich and White, 1980; Holdren and Ehrlich, 1982).

While trying to elucidate patterns of speciation in *Euphydryas*, our research group would like to evaluate behavioral and genetic incompatibilities between these sets of populations, but so far the difference in their phenology has not even permitted us to obtain adults from both populations simultaneously in the laboratory. If we did, and if we could assume that laboratory behavior was the same as behavior in nature (we could not), the results would still not tell us with assurance what would occur if the two became sympatric in nature.

Suppose it became possible for *Euphydryas* once again to occupy the intermountain regions and the agricultural Central Valley of California. If that happened, a completely unpredictable set of ecological and selective events would occur *before* significant opportunity for interbreeding could exist. Populations of *Euphydryas editha* and a wide diversity of potential host plants would reinvade the lowlands from many refugia. The silliness of trying to imagine such a "test" of whether *bayensis* and *gunnisonensis* were conspecific is clear. It would not, in all likelihood, even be possible to identify two groups of *editha*-like butterflies as *bayensis* and *gunnisonensis* descendants.

The basic point is that the California and Colorado *E. editha* are classified in the same species on phenetic grounds—because they look alike, behave alike in many respects, feed on chemically similar foodplants, have similar allozyme genetics, and so forth. Should laboratory tests show some degree of genetic incompatibility—which seems not unlikely on the basis of preliminary intercrossing of other *Euphydryas* populations (Odendaal and Ehrlich, unpublished)—we probably would still continue to consider them conspecific.

Only if it were certain that successful interbreeding is now impossible *and* that compatibility could not be restored by selection during a long period of migration leading to sympatry would we elevate *E. e. gunnisonensis* to specific status. The latter is especially important, since incompatibility today appears largely a matter of asynchrony, which might well evolve back toward synchrony. Taxonomists have always agreed that sexually reproducing populations between which interbreeding is obviously impos-

sible belong to separate species—to our knowledge no one has suggested lumping *E. editha* and *Felis tigris* even though no tests of potential interbreeding have been attempted.

The judgment of impossibility of interbreeding of certain *Euphydryas* populations can be made strictly on phenetic grounds—for color pattern, genital morphology, mating behavior in the laboratory, chromosome behavior in hybrids, fertility in crosses, viability of hybrid offspring fed different larval hosts, and so on, are all aspects of the phenotype. For example, the Colorado *E. editha* can reasonably be considered not to be conspecific with *E. phaeton*. Phenetic analysis, including the behavior of individuals toward one another in the laboratory and allozyme analysis, shows them to fall into very distinct clusters. But this does not involve the application of the BSC—*E. editha* and *E. phaeton* were recognized as distinct *kinds* of organisms long before anyone thought about the BSC.

In short, where two kinds are sympatric and noninterbreeding, or allopatric and very distinct, the BSC adds nothing. Where they are allopatric and not very distinct, it provides no tool—even in theory—for deciding where the species boundaries should be drawn. It is thus useless in practice.

We are, however, in agreement with many points of Shapiro's paper. It is very important for systematists to think evolutionarily, for they are classifying products of evolution, and the patterns those products show in nature throw light on the process. For example, the pattern to be expected under the "punctuated equilibrium" hypothesis (Gould and Eldredge, 1977; Stanley, 1979) would, in most time periods, be quite different from that anticipated under a Darwinian—that is, a more gradual—regime (Lande, 1980). Work now going on in our group indicates a spectrum of levels of differentiation in *Euphydryas*, the kind of pattern one would expect if speciation were constant and gradual. It is our impression that this sort of pattern is common in butterflies, and that the group as a whole shows no sign of speciation stasis.

A reexamination of Ehrlich's 1961 categorization of butterfly genera according to the distinctness of the species contained in them is instructive. If the world were mostly made up of "good species" in the stasis stage of the punctuated equilibrium model of speciation, one would expect to find few genera in which there was any debate about how many species there were and which populations belonged to which species. This is especially true in a group as continually studied as the butterflies—although first-rate biologically oriented studies such as those of Shapiro on *Pieris* make up a depressingly small proportion of the work.

Most of the genera in the 1961 list would remain in the same place today, as a few examples will show. There are still no difficulties with recognizing the Nearctic species of *Nymphalis* as distinct, and still no resolution of the relationship of several of those with European populations. For instance,

what would happen if the North American *Nymphalis milberti*, *N. californica*, and *N. vau-album j-album* became naturally sympatric with the Palearctic *N. urticae*, *N. polychloros*, and *N. vau-album vau-album* is unknown and unknowable. The current nomenclature simply reflects the guesswork of taxonomists who may think they are studying biological species.

The problems with *Papilio* persist, with opinions widely varying on relationships within the *machaon* group. Indeed, a new "species" (*P. joanae*) has been added to the mess since Ehrlich wrote. The relationship of *Papilio glaucus* and *P. rutulus* remains in doubt—some believing they are "good species" and others (J. Scott, pers. comm.) that they are conspecific. *Speyeria*, *Boloria*, *Oeneis*, *Cercyonis*, *Coenonympha*, *Chlosyne*, and so on remain confused, with much rearranging but no appearance of neat clusters.

Results from groups that have been particularly well studied since 1961, such as *Phyciodes* and *Euphydryas* show complexity, not neat biospecies. Populations of *Phyciodes tharos*, for instance, exhibit genetic incompatibility (egg infertility) that gradually increases with distance (Oliver, 1972). Incompatibility between *P. tharos* and *P. campestris* differs only quantitatively from that within *P. tharos* (Oliver, 1978), while crosses between *P. tharos* and *P. batesii* show not only lowered egg fertility but developmental abnormalities as well (Oliver, 1979).

In *Euphydryas* the relationship between closely-related *E. chalcedona* and *E. anicia*, considered conspecific by Scott (1978), is particularly complex. For example, in the Pequop Mountains of northeastern Nevada, black *E. chalcedona nevadensis*, which oviposits on *Symphoricarpos*, flies sympatrically and synchronously, with no sign of interbreeding, with red *E. anicia wheeleri* which oviposits on *Castilleja chromosa*. Black *E. chalcedona olancha* on the east slope of the Sierra Nevada intergrades in genitalic characters and wing color with red *E. anicia wheeleri* on the west edge of the Great Basin. Both oviposit on *C. chromosa*.

The situation in *Lethe* has, as Shapiro points out, become more complex since 1961—although we cannot see any validity to his claim that the biological species concept (as opposed to recognizing that habitat selection is an important aspect of the phenotype) had anything to do with the recognition of the sibling species. No one disputes (or has disputed) that sympatric, synchronic populations that do not interbreed should be considered to belong to separate species (for simplicity, we will ignore the infrequent problem of "circles of races" here).

What Ehrlich predicted was that in cases of sibling species careful numerical phenetic analysis would produce discrete clusters. We know of no test subsequent to Ehrlich's that has been made of that claim, but since Carde et al. (1970), using purely phenetic data, established the specific distinctness of *Lethe appalachia*, Ehrlich's claim still appears to be valid.

In fact *eurydice* and *appalachia* were considered morphologically distinct more than 35 years ago (Chermock, 1947). The subspecific designation of *appalachia*, however, was based on inadequate information. With a type series of only 33 individuals from several states, Chermock mistakenly thought there was an "overlap of diagnostic features." He was wrong; Carde et al. (1970), with many more specimens, found in a survey of 20 phenetic characters that they "differ subtly but consistently."

Shapiro's studies have certainly extended our understanding of *Pieris* since Ehrlich's original paper. As in *Lethe*, differences in phenotypically similar *Pieris occidentalis* and *P. protodice* were noted early, then documented and specific status assigned (Chang, 1963), well before a lack of interbreeding was described in a zone of sympatry (Shapiro, 1975). Shapiro recently admitted (pers. comm.) that he was puzzled about the status of some forms of the *P. napi* complex in North America. The more vexing question of whether Nearctic *P. occidentalis* should be considered conspecific with Palearctic *P. callidice* remains unresolved. Shapiro's (1980) finding of substantial genetic incompatibility between geographically distant Alaskan and French populations is not surprising in view of Oliver's (1972) findings with *P. tharos* and those of our group (Odendaal and Ehrlich, unpublished) on incompatibility within species of *Euphydryas*.

Shapiro's work shows how thinking evolutionarily can enrich our understanding of taxonomic complexes. Thinking evolutionarily, however, is not the same as assuming that butterflies can be divided into biological species, or that "species" would represent the same things in different taxonomic groups, including different groups of butterflies. For example, the old idea that all species in sexually reproducing organisms are evolutionary units bound together by gene flow appear to be incorrect (Ehrlich and Raven, 1969).

We do disagree completely with one of Shapiro's statements—that is, that there is a connection between the biological species concept and the "presumption that phylogeny could be inferred at all." Note that, in Mayr's quoted definition, there is no phylogenetic or historical element; in fact it could be adopted by a creationist! Basically, however, we think there is very little disagreement between our position and that of Shapiro—mostly a terminological difference. We all agree that careful breeding experiments, ecological studies, and laboratory investigations of development under different environmental regimes are most useful in understanding the evolution of butterflies and can lead to enormous improvements in taxonomy around the species level. Shapiro believes that this is applying the BSC; we contend it is simply applying phenetics.

We enthusiastically endorse Shapiro's observation that Darwinism predicts the "fuzziness of species boundaries"—indeed we would go further. Our working hypothesis is that Darwinism predicts a continuum of differentiation from "same population" to "distinctly different species."

We think that approaching nature with the notion that the question "is it a good biological species?" can normally be answered yes or no has biased the view of organic diversity away from a Darwinian (*gradualist*) interpretation!

In summary, we agree with Shapiro that studying the genetic/interbreeding relationships of populations is a useful exercise for systematists, and may often produce information that is useful in making taxonomic decisions. We also believe that the biological species concept once played a very important role in focusing thinking about processes of speciation, and that Mayr's basic view that speciation is primarily allopatric is correct. But, because of the impossibility of defining actual and, especially, *potential* interbreeding, taxonomists do not and cannot use the biological species concept to determine what are or are not "good species"—even if they imagine they are so doing. And in so imagining, they contribute to a biased and basically anti-Darwinian view of the patterns of differentiation found in nature.

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